THE GYMNOSPERM *ARCHAEOPTERIDIUM TSCHERMAKII* AND AN ASSOCIATED GLANDULAR FRUCTIFICATION FROM THE UPPER VISEAN DRYBROOK SANDSTONE OF GREAT BRITAIN

by N. P. ROWE

ABSTRACT. *Archaeopteridium tschermakii* (Stur) Kidston is described from compressions and fusainized material from the Puddlebrook locality of the Drybrook Sandstone of Gloucestershire. Fronds are up to 400 mm long and bifurcate, bearing oval to rounded pinnules on pinnae varying in complexity according to their position on the frond. Pinnules have a prominent surface pattern with several veinlets entering the pinnule base which divide and extend to the pinnule margin. Fusainized pinnules show evidence of longitudinal ridges and furrows, an ornamented cuticle, sunken stomata, veinlets comprising tracheids with circular bordered pits and subepidermal fibre elements with annular or spiral thickenings. Two fronds are associated with twenty-four and eleven synangiate organs respectively. Two isolated synangia are fusainized. Synangia are described as the new genus *Cornutheca* and are cone-shaped with a surrounding wall bearing numerous capitate glands enclosing a central area with 9–75 acuminate, slightly curved sporangia. The synangia are borne terminally on a slender, cruciate branch system. The possibility that *Cornutheca* was the pollen organ of *Archaeopteridium* is discussed and synangium diversity among Lower Carboniferous putative gymnosperms considered.

FOLLOWING the recent advances in our knowledge of seed plant origins and evolution, the fact remains that most of the stems, leaves and reproductive organs known from the Upper Devonian and Lower Carboniferous are identified from isolated organs. Important recent exceptions to this include the known attachment of some of the earliest seed-bearing structures to extensive branch systems (Fairon-Demaret and Scheckler 1987; Rothwell *et al.* 1989) and, higher in the Lower Carboniferous, the median attachment of cupulate organs to dividing petioles (Rowe 1988*c*) and profusely branched sporangiate organs attached terminally to undivided fronds (Skog and Gensel 1980). In addition to these, there are numerous reports of associated gymnosperm organs where leaves, stems and reproductive organs are found close together at the same locality (Kidston 1923; Walton 1931; Jennings 1976; Long 1979*a*, 1979*b*; Rowe 1988*c*) and where identity between pollen and seed organs with stems and foliage has been suggested. Recent findings have shown that many permineralized and compression floras contain diverse assemblages of gymnosperms and that reconstruction from isolated plant organs by association will lead to erroneous reconstructions. In spite of this some authors have attempted graphic whole-plant reconstructions of Early Carboniferous plants using published data which only suggest identity between 'associated' plant organs (Retallack and Dilcher 1988). The following account reports a situation where a type of foliage and reproductive organ are closely associated but not in connection.

Archaeopteridium tschermakii (Stur) Kidston is one of many Lower Carboniferous foliage compressions known only from isolated petioles, secondary rachises, isolated pinnae and pinnules. The following account attempts to elevate the limited concept of this frond by identifying a size range of nearly complete fronds to demonstrate pinna/pinnule variation in a single fossil species, by demonstrating fine morphological information of leaf morphology/anatomy from fusainized material and by describing a complex synangiate organ and its extensive branch system which is closely associated with two specimens of frond.

Kidston (1923) founded the genus *Archaeopteridium* and gave a detailed diagnosis for the species

[Palaeontology, Vol. 35, Part 4, 1992, pp. 875–900, 4 pls.]

A. tschermakii. He eliminated any possibility that the material first described by Stur (1875) belonged to *Archaeopteris* Dawson, 1871 from the Devonian of Canada and also dismissed any connection between Stur's material and *Archaeopteris* from the Devonian Kiltorcan flora in Ireland (Johnson 1911). Stur (1875) illustrated five specimens of which two are large bifurcate fronds up to 350–400 mm long. He divided the material into two species; *Archaeopteris tschermakii* and *Archaeopteris dawsoni*, the latter distinguished by a greater degree of lobation in its pinnules.

Kidston (1923) figured only two Scottish specimens of *Archaeopteridium tschermakii* which he referred to in detailed description and comparison but did not figure Stur's original material from Poland. Kidston's material includes the upper part of a secondary rachis (Kidston 1923, pl. 40, fig. 3) with approximately twelve alternate pinnae. He illustrated pinnae from the distal (pl. 41, fig. 2) and proximal (pl 41, fig. 1) parts of this rachis to demonstrate the pinnule variation of one frond. On this basis he recognized only one species of Stur, for which he selected *Archaeopteridium tschermakii* as the type species.

Secondary rachises of *A. tschermakii* show a superficial resemblance to the axes comprising the ultimate leafy branch systems of the Upper Devonian progymnosperm *Archaeopteris.* The similarities include: oval, sometimes slightly lobed pinnule margin, the apparently pinnate organization of the *Archaeopteris* branch system and the venation of the pinnules which consist of several veinlets entering the base of the pinnule and which divide two to four times. It was these apparent similarities that led to the presumed identity between Stur's Lower Carboniferous fronds and Dawson's Upper Devonian branches of *Archaeopteris.* In fact, isolated pinnae fragments of *Archaeopteridium* poorly preserved as compression would be distinguished only with difficulty from similarly preserved *Archaeopteris*.

The overall frond architecture of *Archaeopteridium* distinguishes it immediately from *Archaeopteris* by (1) a bifurcate frond morphology dividing the frond into two equal segments (2) the expanded petiole base and reduced petiolar pinnae (3) the lack of rachial pinnules attached to the rachis at the same level as the penultimate rachises. Also, as pointed out by Kidston (1923), a further difference distinguishing *Archaeopteridium* is the lack of sporangiate sporophylls which characterize fertile branch systems of *Archaeopteris*.

Lele and Walton (1962, pl. 21, fig. 22) illustrated a single pinna with ten to twelve alternate, oval pinnules which they assigned to *Archaeopteridium tschermakii*. This material came from the Drybrook Sandstone flora at Puddlebrook and was the last illustrated record of the foliage since Kidston's monograph apart from brief reports of the species from the Lower Carboniferous of Silesia (Migier 1971) and Moravia (Purkyňová 1975).

The compression flora at Puddlebrook is Upper Visean (Asbian, NM Biozone) and contains a diverse assemblage of lycophytes (Thomas 1972; Thomas and Purdy 1982; Rowe 1986), including herbaceous forms (Rowe 1988*a*) and sporophylls (Allen 1961), and gymnospermous stems, leaves, cupules and synangia (Lele and Walton 1961; Rowe 1986, 1988*c*). Most elements of the flora are preserved in a variety of ways as 'flattened compressions', 'three-dimensional impressions' (Rowe 1988*b*) and as fusainized material which, in some cases, is believed to represent fossil charcoal. A combination of techniques in comparing and correlating differing preservation types has aided the three-dimensional reconstruction of plant organs and provided fine morphological and some anatomical details. Both the frond and synangiate organ described here are preserved as flattened compression, three-dimensional impression and fusain.

MATERIAL AND METHODS

Compression and impression material was observed and photographed using cross polarized light. Fusainized material was routinely mounted on stubs and observed with the SEM. Although this technique afforded reasonable fine details, the overall organization of the pollen organ was studied better by a modified preparation of embedding and sectioning.

Specimen V.63527 was photographed first while still partly embedded in the matrix (Text-fig. 4c). The specimen and surrounding matrix was first heated gently and when left to cool an initial application of low viscosity cyanacrylate adhesive was allowed to penetrate the specimen. The specimen was then embedded in a small block of polyester resin and sectioned serially using a 0·3 mm diameter 'Buehler' wafering blade. Wafered sections had an average thickness of 0·7 mm and were 0·32 mm apart. The sections were ground and each surface was polished using a series of carborundum abrasives. Some sections were left as opaque wafers for observation with reflected light and others were ground into transparent thin sections for observation with transmitted light.

The material described in this paper is deposited in the Natural History Museum, London with the serial numbers V.63489–V.63528.

DESCRIPTION OF FROND

Archaeopteridium tschermakii is a rare element in the Drybrook Sandstone flora and represented only by about fifty specimens. Cuticle is not preserved in compression material which consists of faint impression surfaces slightly darker than the surrounding matrix. Only very fine particulate organic material remains on the impression surface – a type of preservation found commonly among other plant groups at the locality (Rowe 1988*a*, 1988*b*, 1988*c*).

Morphology of frond

The terminology used to describe these fronds comprises the following; a petiole or primary rachis undergoes a division to produce two secondary rachises. Pinnae are borne suboppositely on the primary and secondary rachises and comprise subopposite to alternate pairs of pinnules. In this account the term pinnule is proposed to represent the discrete laminate portions of the pinnae each of which is demarcated proximally by the contraction of the lamina into a non-laminate stalk. In cases where a single laminate unit is lobed or partly divided the constituent parts are referred to as pinnule segments.

Four specimens show the connection of secondary rachises to petioles (Table 1) and demonstrate the variation in overall size, width of primary and secondary rachises and size of pinnules (Pl. 1, figs 1, 3).

Nearly all of the petiole is preserved in one of the smaller fronds (Pl. 1, fig. 1) which is 27 mm long and 2·4 mm wide in the middle. The base of the petiole is expanded and approximately one half to one third of the secondary rachises are still attached. Pinnae on the petiole are minute and the internodal distance between subopposite pairs is only 1 mm. In V.63492 (Pl. 1, fig. 3) the petiole is at least 70 mm long and 4·2 mm wide in the middle. The secondary rachis on the right is 155 mm long, nearly complete and bears large, complex pinnae. The petiolar pinnae become increasingly complex towards the division of the frond and have internode lengths of 16–17 mm.

Morphology of pinnae

Pinnae attached to the petiole in small and large fronds (Table 1) show a gradual increase in size towards the division of the frond. The morphological transition of pinnae from the petiole to the secondary rachises is not a simple gradational series. The first pinnae on the secondary rachises in V.63492a are simpler and smaller than the most distal pinnae on the petiole (Pl. 1, fig. 3; Table 1).

Pinnule segments in large median pinnae of secondary rachises most frequently have lobed margins (Pl. 1, figs 2–3). The overall size of pinnae on a single secondary rachis may vary from 16 × 12 mm proximally to 61 × 20 mm medianly (Table 1). Pinnae on the lower to median position of the secondary rachis of small fronds are 7·9 × 4·2 mm.

Pinnae are positioned suboppositely on both petiole and secondary rachises. Internode lengths between subopposite pairs vary according to position on the frond (Table 1). Internode lengths shorten towards the dichotomy on the petiole but, on the secondary rachises, increase towards the median part of the frond and then decrease distally (Pl. 1, fig. 3; Table 1). There is some indication that pinnae on the inward-facing side of each secondary rachis are smaller than those at equivalent levels on the outer-facing side (Pl. 1, fig. 3).

Individual pinnules range from 1·3 × 0·8 mm to 4 × 2·5 mm in small fronds to 10 × 4 mm to 15 × 8 mm in large fronds. 3–20 pinnules are arranged suboppositely to alternately on pinnae and are oval to obovate with attenuated, decurrent bases connecting them to the rachis (Pl. 1, figs 2, 4). Pinnules on the petiole, particularly towards the base, have a more rounded outline. In V.63492 the number of pinnules on each pinna on the secondary rachis increases from 4 to 18 and then declines distally to about 9 (Table 1).

Characters which remain proportionately constant between frond sizes include relative pinna dimensions in relation to position on the petiole and secondary rachis and pinna internode lengths (Table 1). In all the fronds

TABLE 1. Quantitative measurements of nearly complete fronds of *Archaeopteridium tschermakii*. All values are in mm (pro., med. and dis. refer to proximal, median and distal positions on secondary rachises and petioles).

	Specimen no.				
	V.63490	V.63489	V.63498	V.63497	V.63492
Total length	> 54	> 57	> 85	> 160	> 225
Petiole length	> 16	27	> 58	> 80	> 70
Petiole width	2·6	2·4	3·5	3·1	4·2
2° rachis length	> 15	> 30	> 25	> 80	> 155
2° rachis width	1·8	1·7	2	2	2·5
Internode length (Pinnae on petiole)	—	1	7·5	> 15	16·5
Petiole pinna size	—	2·4 × 1·4	8 × 9	14·5 × 11	dis. 15 × 11·5 11·5 × 10 pro.
2° rachis internode length	dis. 11·2 9·2 pro.	6·2	—	2nd–3rd pinnae ⩾ 15	dis. 11 14 16 20 22 25 17 15 pro.
2° rachis pinna dimensions	dist. 3·9 × 11·8 4·6 × 12·4 2·8 × 8·5 pro.	med. pinna 7·9 × 4·2	pro.–med 15 × 9	pro. ⩾ 28 × ⩾ 10	dis. 25 × 8·5 27 × 9·5 35 × 11 44 × 10 56 × ⩾ 10 61 × 20 61 × 18 22 × 14 16 × 12 pro.

observed, pinna size and internode length increase towards a maximum in the middle region of the secondary rachis and then decreases towards the apex (Pl. 1, fig. 3).

Depending on the size of pinnule, 3–8 veinlets visible on compressions enter the decurrent base at an acute angle to the rachis (4°–5°). They are 0·08–0·1 mm wide and divide 2 to 3 times at acute angles (Pl. 1, fig. 4). Veinlets extend to the pinnule margin and change in angle from 10° to 35° from the rachis. The veinlets may be slightly curved in the last few millimetres towards the margin where they are 0·4 to 0·65 mm apart.

EXPLANATION OF PLATE 1

Figs 1–4. *Archaeopteridium tschermakii*, Forest of Dean, Upper Visean. 1, V.63489a, small bifurcate petiole with enlarged base and minute petiolar pinnae. Pinnae on secondary rachises are smaller and less complex than those of larger fronds, × 1·7. 2, V.63493a, four pinnae attached to median portion of 2° rachis. Pinnules are oval at base of pinna becoming lobed medianly and simple again distally, × 1·4. 3, V.63492a, medium sized, bifurcate petiole with nearly complete secondary rachis on right. Pinnules on petiole are simple, × 0·9. 4, V.63494a, distal pinnules of pinna on secondary rachis. Pinnule bases are decurrent with pinna rachis. Approximately 5 veinlets enter each pinnule base and extend to the pinnule margin, × 3·0.


1


3


2


4

ROWE, *Archaeopteridium*

In some cases the pinnule margins are frayed, presumably as a result of microbial degradation and/or mechanical damage.

In summary, large fronds bear larger pinnae with longer internodes. The pinnule nervation and the relative sizes and internodes of pinnae and pinnules remain constant between large and small fronds.

Fine morphology of pinnules (fusainized material)

One fusainized pinnule fragment provided fine details when observed by SEM (Pl. 2, fig. 1) and is identified with compression foliage of *Archaeopteridium* on the following grounds; (1) The shape and size of the fragment and its impression on the matrix (V.63520a) correspond to the lower half of an *Archaeopteridium* pinnule. (2) The number, angle and degree of separation of ridges on the pinnule equate to strands of organic material constituting the nervation on compressions. (3) There is no other type of pinnule with this type of shape and nervation from the Drybrook Sandstone flora.

Both surfaces were observed by SEM. One is presumed to represent the abaxial surface with a well-preserved epidermis (Pl. 2, figs 1–4). The fragment represents the fan-shaped, lower half of a pinnule with 6–8 longitudinal ridges separated by grooves. The epidermis consists of sinuous, longitudinally aligned, elongate cells, 66 × 20 mm–190 × 24 μm with tapered end walls. Epidermal elements are conspicuously shorter around stomatal apertures (Pl. 2, figs 2–3) which are confined to the grooves and are 32–40 μm long and 6–8 μm wide. They are orientated parallel to the ridges. The outermost layer visible on the epidermis is finely sculptured with a reticulate pattern of broad, flattened projections (Pl. 2, figs 3–4). A fractured transverse section indicates that this is 1·5 μm thick and is continuous over the periclinal surfaces of the epidermal cells and is interpreted as preserved fusainized cuticle (Text-fig. 1B). Beneath the epidermis two types of ornamented cell are visible including longitudinally aligned elements, 100–140 × 25 μm with scalariform to spiral thickenings (Pl. 2, fig. 6, lower element) and others with less regular thickenings (Pl. 2, fig. 6, upper element) and might represent sclerenchymatous elements surrounding the tracheids or comprising the hypodermis.

The strands of tracheids (60 μm) wide have 8–10 elements and divide equally. Individual tracheids are at least 80 μm long and 8 to 12 μm in diameter. The ornamentation consists of annular thickenings or circular bordered pits on all surfaces of the tracheid wall (Pl. 2, fig. 5). An additional structure is observed on the pinnule surface which resembles fungal hyphae. These are approximately 6 μm wide and extend across 3 ridges on the pinnule surface (Pl. 2, fig. 2). It is of interest that one of the 'hyphae' appears to enter one of the stomata (Pl. 2, fig. 3).

The 'adaxial' surface apparently lacks stomata and consists of elements 80–140 μm long and 8–16 μm wide. The ridges and grooves (Text-fig. 1A) are not as strongly developed as on the abaxial surface. A cuticular layer is present on the adaxial surface which shows evidence of 'blistering'. This takes the form of circular to oval sunken areas approximately 5–40 μm on the cuticle surface which are delimited from the rest of the cuticle surface by a smooth rim (Text-fig. 1A). This feature has been observed in experimentally charred leaves (A. C. Scott pers. comm.) and provides further evidence of a wild fire origin of fusainized material at the Puddlebrook locality.

SYSTEMATIC PALAEONTOLOGY

Class Gymnospermopsida (*sensu* Stewart 1983)
Order LYGINOPTERIDALES (*sensu* Barnard and Long 1975)
Family INCERTAE SEDIS
Genus ARCHAEOPTERIDIUM Kidston, 1923

EXPLANATION OF PLATE 2

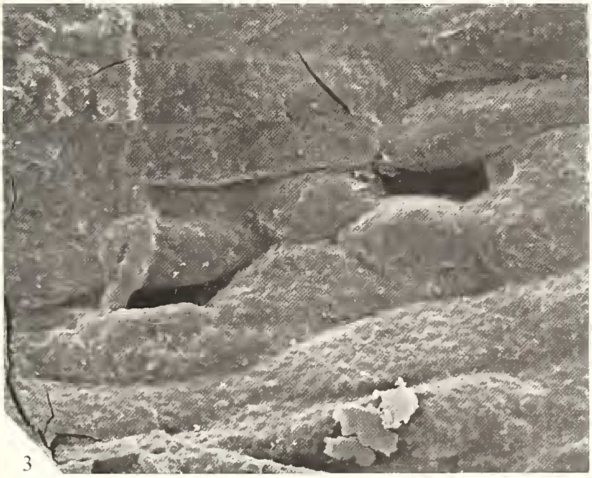
Figs 1–6. *Archaeopteridium tschermakii*, Forest of Dean, Upper Visean V.63520a$1. 1, 'abaxial' surface of fusainized pinnule with axially aligned ridges and grooves, × 20. 2, surface of 'abaxial' epidermis with ridges and furrows. Stomatal apertures are axially orientated and apparently confined to furrows. Note strand-like material resembling fungal hyphae, × 180. 3, two stomatal apertures each surrounded by 4–5 shortened epidermal cells. Note entry of 'hypha' into aperture, × 500. 4, surface of pinnule surrounding stomatal aperture. The cuticle surface is sculptured, × 1700. 5, part of veinlet in proximal part of pinnule showing tracheids with circular/oval pits and annular thickenings, × 1100. 6, sub epidermal, sclerenchymatous tissue beneath ridge with annular-spiral thickenings, × 500.

1

4

2

5



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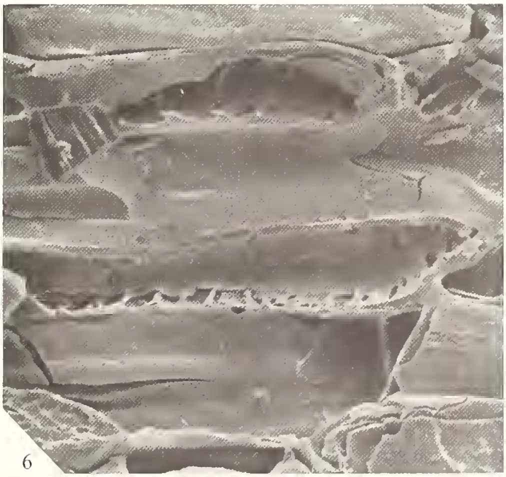

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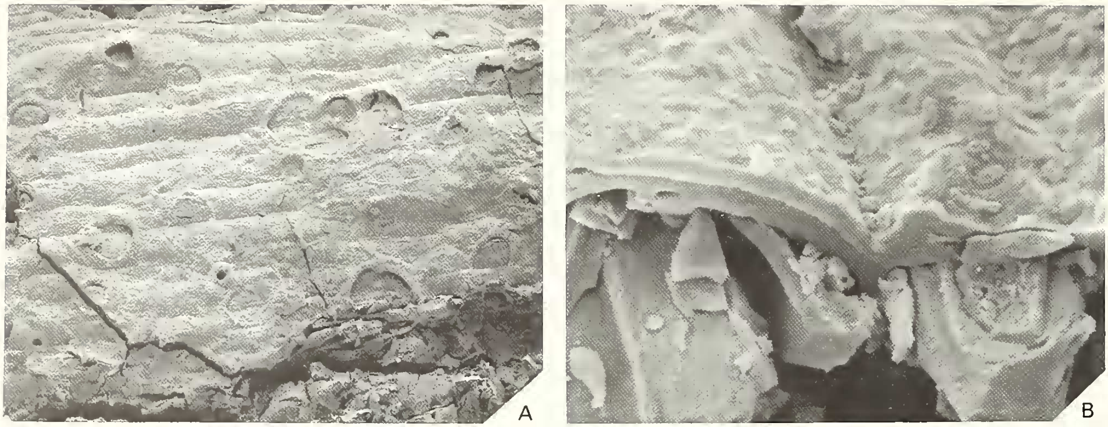
ROWE, *Archaeopteridium*



TEXT-FIG. 1. Fusainized pinnule segment of *Archaeopteridium tschermakii*, V. 63520a $2. A, 'adaxial' surface of lamina showing longitudinal ridges and blistering effect on the cuticle, × 240. B, Transverse fracture surface of cuticle (outermost layer) and anticlinal and periclinal cell walls of the epidermis. The cuticle has a grainy texture in comparison with the surface of the cell walls, × 1100.

Type species. Archaeopteridium tschermakii (Stur) Kidston, 1923 from the emendation of genus *Archaeopteridium*.

The diagnosis of *Archaeopteridium* given originally by Kidston is emended here to accommodate the new morphometric information from different sized fronds and the fine structural information from fusainized material based on specimens described here from the Puddlebrook locality at Drybrook. The emended diagnosis accommodates both the genus and the species. *A. tschermakii*.

Emended diagnosis. Fronds, small (55 mm long) to large (350–450 mm long), bifurcate consisting of petiole with expanded base and pair of lanceolate secondary rachises. Pinnae alternate to subopposite on petiole and secondary rachises. Petiolar pinnae simple proximally, becoming complex distally. Pinnae on secondary rachises simple proximally, complex medianly becoming simple again distally. Pinnules alternate, rounded on petiolar pinnae, oval and decurrent on secondary rachises, occasionally lobed in distal third of margin on larger pinnules of median pinnae of secondary rachises. Venation characterized by 3–8 veinlets (80–100 μm wide) entering pinnule base at acute angle (4°–5°) to rachis, undergoing 2–3 divisions, extending to pinnule margin and changing in angle to 10°–35° from rachis. Surfaces of pinnule comprising alternate longitudinal ridges and grooves, less well developed on adaxial surface. Abaxial surface comprising cuticle 1·5 μm thick with coarse reticulate ornamentation, epidermal elements 66×20 μm to 190×24 μm. Stomatal apertures 32×6 μm to 40×8 μm surrounded by 3–6 shorter epidermal cells. Veinlets, approximately 8–10 cells (60 μm) wide proximally. Tracheids, 8–12 μm diameter, at least 80 μm long with multiseriate circular, oval bordered pits or annular wall thickenings.

Archaeopteridium tschermakii Stur, 1875 emend.

Plates 1–2; Text-figs 1–2

1875	*Archaeopteris Dawsoni* Stur, p. 60, pl. 12, figs 2, 2b, 3–4.
1875	*Archaeopteris tschermaki* Stur, p. 57, pl. 12, fig. 1; pl. 16, fig. 11.
1923	*Archaeopteridium tschermaki* Stur; Kidston, p. 182, pl. 40, fig. 3; pl. 41, figs 1–2; (see also synonymy therein).
1962	*Archaeopteridium tschermaki* Stur, Lele and Walton, pl. 21, fig. 22.

Material. Emendation substantiated by specimens: V.63489, V.63490a–b, V.63492a–b, V.63493, V. 63494, V.63520a$1–2.

Occurrence. Lower Carboniferous of Europe. Upper Visean of Forest of Dean, Gloucestershire, Western England; Lower Limestone Group, Oil Shale Group of Scotland (see Kidston 1923); Culm (U. Visean) of Poland (see Stur 1875); Silesia and Moravia (uncorroborated reports, see Migier 1972, Purkyňová 1975)

RECONSTRUCTION, COMPARISONS AND DISCUSSION

Two fronds of *A. tschermakii* are reconstructed in Text-figure 2 demonstrating the range of foliage variation observed in the Puddlebrook assemblage. Both reconstructions are based on nearly complete frond specimens. Less complete fragments can be identified with specific areas of variation observed on a single frond. In this way, for example, a specimen comprising a narrow rachis with alternate, minute rounded pinnules could be interpreted as the petiole of a small frond and, one showing large slightly lobed oval-shaped pinnules, could be assigned to the area of large well developed pinnae in the middle position of a large frond. The list of measurements in Table 1 includes more data such as increasing/decreasing internodes, widths of rachises etc. which also demonstrate similarities between different size groups of whole fronds.

One of the problems in carrying out quantitative morphometric analyses on frond compressions is the fact that measurements of width and length of pinnae, pinnules and their exact position of departure from the rachis are vulnerable to inaccuracy owing to imperfect preservation such as folding, twisting, partial fragmentation and weathering. This is coupled with the relatively low availability of whole specimens which results in quantitative measurements showing large ranges from small samples.

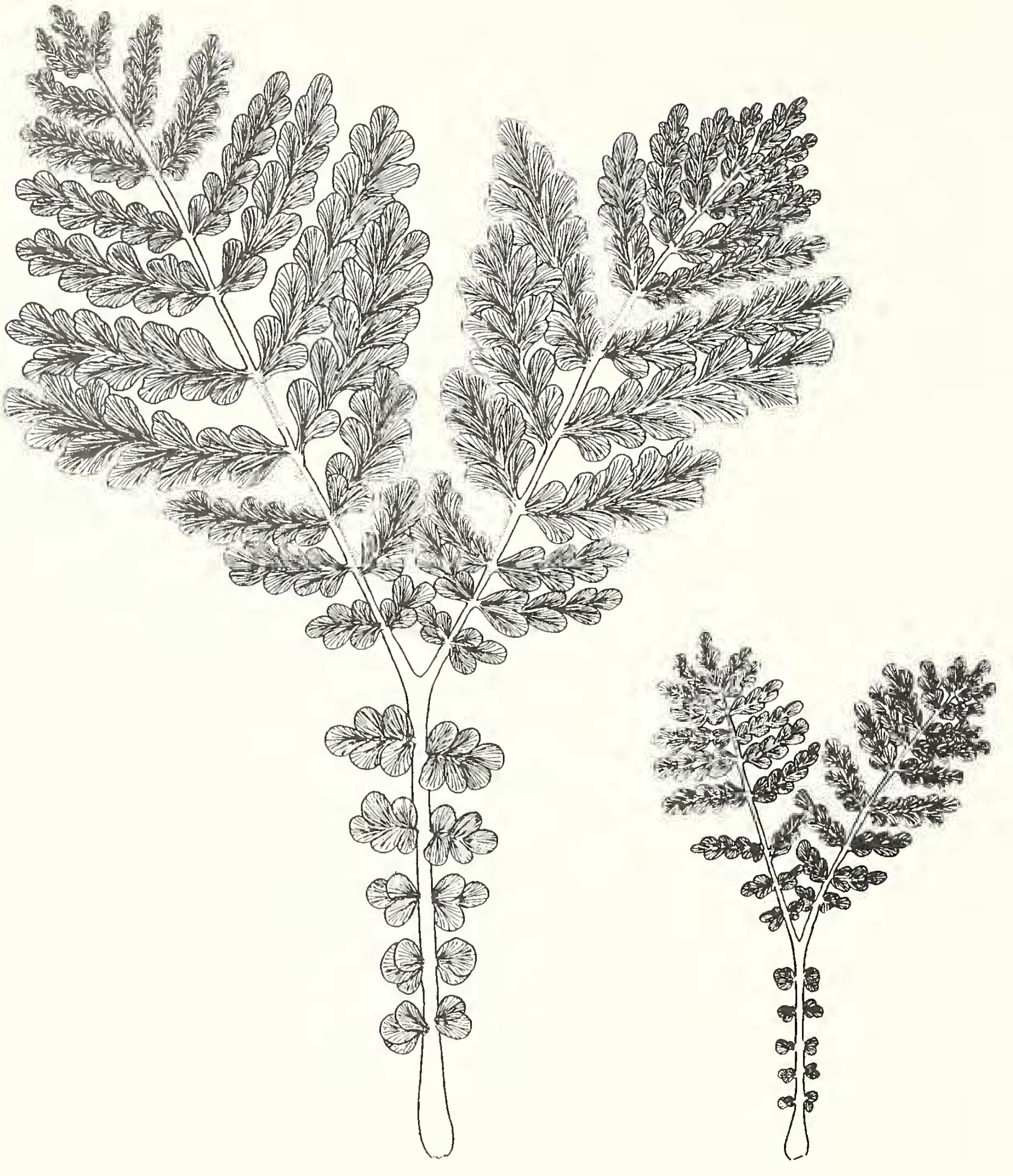
The material described here corroborates Lele and Walton's (1962) identification of the British material as the same as that described and illustrated by Stur (1875) from Central Europe. This is partly because the pinnule morphology of this particular foliage is very characteristic. With many other Lower Carboniferous foliage types preserved as compressions a realistic identification based on the fragmentary material available to Lele and Walton would have been impossible. The nearly complete fronds described here are more similar to Stur's than any other described frond with regard to pinnule variation on the whole frond. Secondly, the pinnule morphology as well as the pinna variation described by Kidston in material from Scotland also fits well with that observed in the material described here. For these reasons the Drybrook material is assigned to *A. tschermakii*.

Many Lower Carboniferous foliage compression genera have been known since the middle of the last century. A number of these are bifurcate and consist of petioles which divide to give a pair of pinnate to multi-pinnate secondary rachises. Others do not bifurcate and examples of these may be distinguished relatively easily from *Archaeopteridium*. The most comprehensive work describing and listing many of these forms, particularly from Great Britain, remains that of Kidston (1923). From a biological viewpoint almost all are provisional form genera.

Other characters that have been used to group and separate genera and species include: overall shape of frond, divisions of rachises, shape and attachment of pinnae and pinnules and degree of subdivision, and extent, direction and type of division of veinlets constituting the nervation. In addition to these, other features include the transverse 'bars' or longitudinal 'striations' on the surfaces of rachises which were believed to represent either sclerotic nests in the cortex or an outer sparganum cortex respectively, both of which are characteristic of many anatomically preserved gymnosperm stems and rachises.

Apart from a few cases where pinna/pinnule morphology is particularly distinctive (*Archaeopteridium* could be considered one of these) the pinna/pinnule morphologies of many Lower Carboniferous fronds intergrade or overlap between currently recognized genera and species. This is aptly demonstrated by the descriptions and illustrations of Kidston (1923) among genera such as *Sphenopteridium*, *Telangium* (*sensu* Kidston 1923), *Spathulopteris*, *Adiantites*, *Plumatopteris*, *Diplotmema* and *Rhodea*.

Triphyllopteris is a widespread Lower Carboniferous foliage type with pinnae rather similar to *Archaeopteridium* comprising oval to slightly subdivided pinnules with numerous parallel veinlets.



TEXT-FIG. 2. Reconstructions of small and medium to large fronds of *Archaeopteridium tschermakii*, × 1.

The major difference separating this foliage is the overall frond architecture which comprises non-bifurcate, vegetative pinnate fronds. Furthermore, the fertile morphology of *Triphyllopteris uberis* from the Lower Carboniferous of the USA consists of a branched axis bearing sporangia, the distal part of an otherwise unbranched frond (Skog and Gensel 1980). Similar vegetative and fertile morphologies separate non-bifurcate fronds of *Rhacopteris* from *Archaeopteridium*. The differences seen in the *Rhacopteris/Triphyllopteris* type of frond architecture comprising branched sporangiate organs contrast with many other bifurcate fronds and may indicate one possibility of distinguished fern or some progymnosperm foliage from that of gymnosperms.

In terms of overall frond morphology, all of these are apparently bifurcate and consist of a petiolar region and a pair of secondary rachises. Within this basic morphology various authors have applied a range of differing interpretations to distinguish frond types. Kidston (1923) separated *Sphenopteridium* from *Spathulopteris* on the grounds of the former having transverse notches and longitudinal striations on the rachises and the latter being smooth. Further specific distinctions are based mostly on the shape and organization of individual pinnules and venation. Other authors had a much broader concept of *Sphenopteridium* including in it many frond types not having ridges and striations.

The main elements of the frond architecture displayed by *Archaeopteridium* include: bifurcate vegetative frond; petiolar pinnae simple, increasing acropetally in size; first proximal pinnae on secondary rachides smaller than most distal pinnae on petiole; pinnae on secondary rachis increasing in size acropetally to middle position of rachis and then decreasing in size towards apex of rachis. This frond architecture is found in a large number of Lower Carboniferous frond types showing a wide range of pinnule morphologies and is found in specimens attributed to *Sphenopteridium*, *Spathulopteris*, *Adiantites* and *Telangium* (*sensu* Kidston 1923). Of significant interest is the fact that this morphology is seen in all known specimens showing a trifurcate, fertile frond morphology to which Walton (1931) gave generic significance in erecting the genus *Diplopteridium*.

Not all frond types with a basic bifurcate morphology conform to this overall organization. *Diplotmema* (Kidston 1923) has no petiolar pinnae and shows a different size distribution of pinnae on each secondary rachis with the largest pinnae occupying the most proximal positions on the secondary rachis and a gradual decrease in size acropetally.

Another divergent frond architecture is seen in *Telangium affine* (*sensu* Kidston 1923) which bears only a single pair of large subopposite pinnae below the division of the rachis, and shows a major bifurcation occurring towards the base of each secondary rachis.

Variations in general frond architecture also include the positioning of smaller pinnae on the 'inner' side of each secondary rachis. This is shown to some extent in *A. tschermakii* from Puddlebrook (Pl. 1, fig. 3) and is described in whole fronds from other genera in material described as *Sphenopteridium pacchyrachis* (Kidston 1923).

In terms of pinna and pinnule morphology, enormous variation is seen among Lower Carboniferous fronds showing otherwise similar bifurcate, petiolate morphology, perhaps the most widely employed character in distinguishing species and genera of foliage. Fronds with narrow, highly divided pinnule segments have often been assigned to the genus *Rhodea* and those showing very narrow pinnule bases at their point of attachment to the rachis which then broaden distally into either oval/rounded or wedge-shaped laminae have been assigned to the genus *Adiantites* (*sensu* Kidston 1923). What is of interest is that highly variable pinnule/pinna types may be borne on fronds with otherwise very similar overall frond architectures. An example of this is the morphology of vegetative fronds of *Diplopteridium holdenii* which have highly divided pinnule segments but show many features in overall architecture similar to *Archaeopteridium* with quite different pinnule types. Similarities include: bifurcate frond; petiolar pinnae with acropetal increase in size/complexity; secondary rachises with the largest and most complex pinnae situated in the middle position of the frond.

Current identification of Lower Carboniferous foliage types and fronds almost entirely consist of simple assignations to provisional form genera and the division of these into arbitrarily defined species. Many of the characters used by numerous authors entailing frond morphology, pinna/pinnule morphology overlap and ontogenetical and phenotypic differences have gone unobserved in the variation of forms described and assigned to Linnean binomials. It is believed that there is more potential information from frond compressions in the fossil record as biological entities than is currently extractable from the currently used lists of form genera and species. This involves identification of whole fronds with a recognizable architecture showing a range of phenotypic/ontogenetical variation; the range in pinna/pinnule morphology seen within this; and, whenever possible, the mode of attachment and nature of reproductive organs. It is believed that such data will enhance or refute current approaches using form genera and species of foliage as indicators of stratigraphy and palaeogeographical flora distributions in addition to systematic and evolutionary studies.

DESCRIPTION OF SYNANGIUM

The following section deals with a fertile branch system closely associated with fronds of *Archaeopteridium*. Two specimens comprise slender branch systems which surround or are superimposed on vegetative fronds (Text-fig. 3A–B). A total of 39 individual synangia are known of which 25 are associated with a frond in specimen V.63525a–b (Pl. 3, figs 1–2) and 11 in specimen V.63526a–b (Text-fig. 4A). Three isolated specimens include fusainized synangia which could be correlated with specimens preserved as impressions and which provide corroborative information on the morphology and fine structure of the fructification (Pl. 4, figs 1–5; Text-fig. 6).

Text-figure 3 combines information from part and counterpart of two specimens (V.63525a–b; V.63526a–b). The outline of each counterpart has been reversed and incorporated on that of the part.

Extensive 'degagement' was necessary to expose the fertile branch system and interconnected synangia.

Branch system organization and relation to vegetative fronds

V.63525a–b. The frond represents the distal two thirds of two adjacent secondary rachises (Pl. 3, figs 1–2; Text-fig. 3A, [R_1, R_2]). The pinnae from both rachises are orientated in one direction indicating that the frond was folded over at the time of deposition so that some of the pinnae lie in the matrix beneath.

On the counterpart (Pl. 3, fig. 2) part of a divided petiole bearing small pinnae is visible on the lower edge of the specimen (P, arrow). This is separated from the rest of the frond by a gap of 11 mm where part of the matrix is missing. The orientation of the petiole fragment with the rest of the secondary rachises suggests that all was part of a single bifurcate frond which became disarticulated during deposition.

On the part (Pl. 3, fig. 1) 16 synangia (nos 1–16) are located on the right of the frond and another 9 (nos 17–25) on the opposite side of the frond (observed on the right side of the counterpart, Pl. 3, fig. 2). Synangia nos 1–8 are borne terminally on a slender branch system. The remaining 8 synangia, just to the left, are interconnected but part of the matrix is missing and they are separated from the main branch system.

The area occupied by both groups of synangia (nos 1–16) is approximately 55 × 50 mm. The complete, interconnected segment of the branch system containing synangia (nos 1–8) occupies a symmetrical, rectangular area approximately 20 × 42 mm. The eight synangia (nos 17–24) on the other side of the frond occupy a similar area and most probably represent an equivalent segment of fertile branch system.

The proximal internode of the fertile axis is at least 18 mm. This axis undergoes four T-shaped divisions. This is seen most clearly in the branch system leading to synangia nos 5–8 (Pl. 3, fig. 1; Text-fig. 3A). The initial

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EXPLANATION OF PLATE 3

Figs 1–5. *Cornutheca glandulosa* gen. et sp. nov., Forest of Dean, Upper Visean. 1, V.63525a, holotype (part), slender axis undergoing four dichotomies and bearing (on right of specimen) 8 terminal synangia. Group of additional 8 synangia on left of specimen orientated towards branch system proximally but separated from second internode by broken matrix. Part of two secondary rachises of an *Archaeopteridium* frond are partly superimposed by the fructification, × 1·3. 2, V.63525b, holotype (counterpart), the left of the specimen contains counterpart impressions of synangia nos 9–16 which are also present on the part V.63525a. The right of the specimen contains a further 4 pairs of synangia (nos 17–24) and a fragment of one more (no. 25) which are not found on V.63525a ('P' arrow points to fragment of divided petiole of *Archaeopteridium* with attached petiolar pinnae), × 1.4. 3, V.63526*a*, proximal surface impressions of three synangia (28*a*, 29*a*, 30*a*) showing rugose synangial surfaces in connection with synangial stalks. Broad based capitate glands are visible around the periphery and on the impression surface where the bases are visible entering the matrix as lobed fissures, × 3·4. 4, V.63526b, distal surface impressions of the same three synangia in fig. 3 (28*b*, 29*b*, 30*b*) and approximately half of two neighbouring synangia (26*b*, 27*b*). The impression surfaces contain numerous pit-like depressions which mark the positions of sporangia entering the matrix, × 3·3. 5, V.63525b, lateral surface impressions of pair of partly superimposed synangia (17*b*, 18*b*). The outline of the synangia is cone-shaped. Capitate glands can be seen around the periphery and as fissures marking the surface. Numerous sporangia are visible as dense tooth-like impressions extending from the distal edge, × 4·5.

PLATE 3


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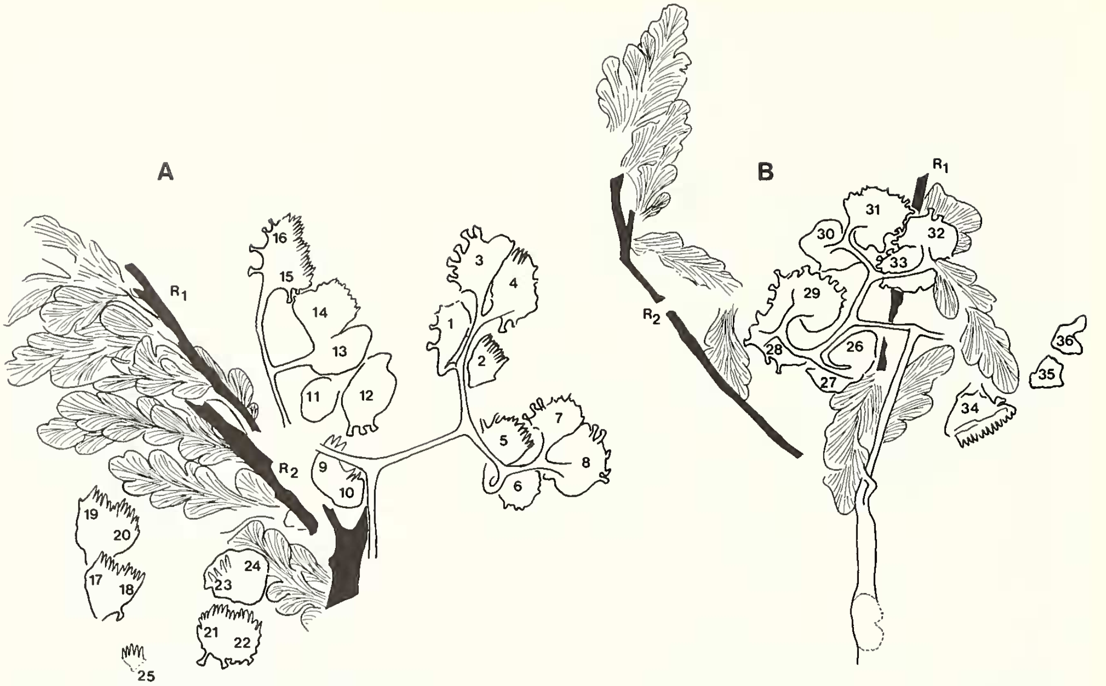
ROWE, *Cornutheca*



TEXT-FIG. 3. Simplified diagrams of part/counterparts of two specimens consisting of extensive branch systems of *Cornutheca glandulosa* with bifurcate fronds of *Archaeopteridium tschermakii*. Numbers refer to individual synangia on separate specimens. Vegetative petioles and secondary rachises ($\mathrm{R}_1, \mathrm{R}_2$) are shaded black. A, holotype, V.63525a–b, × 1·0. B, V.63526a–b, × 1·0.

three divisions result in internodes that are 14, 8 and 5 mm respectively and are separated by similar wide angles. The final division is more acute and separates the synangia into pairs. The terminal parts of the axis enlarge forming the cone-shaped synangia approximately 2–3 mm after each final division.

The penultimate internodes leading to synangia nos 3, 4 and 7, 8 (Text-fig. 3A) are clearly visible but each opposite, penultimate internode leading to 1, 2 and 5, 6 has been compressed/distorted and is not observed well (Pl. 3, fig. 1). The penultimate internode leading to synangia nos 1 and 2 is attached to the axis proximally but is bent back towards the branch and attached to the pair of synangia which superimposes the axis. This is clearly shown at an earlier stage in the uncovering procedure where the proximal parts of the synangium pair disappear into the matrix below. A similar arrangement is observed in the connection of synangia nos 5 and 6 to the branch system.

V.63526a–b. The second specimen consists of a group of interconnected synangia which superimposes a pair of converging secondary rachises (Text-fig. 3B; Text-fig. 4A–B). One of the rachises (Text-fig. 3B[R_1]) passes through the centre of the specimen and bears 4 irregularly orientated and distorted pinnae. Much of this rachis had to be removed to expose the synangia below. The second rachis (Text-fig. 3B[R_2]) is more complete and comprises relatively small pinnae comparable to a small to medium-sized *Archaeopteridium* frond. The upper two thirds of the rachis [R_2] is visible on the counterpart (V.63526b, Text-fig. 3B[R_2]) and the proximal 20 mm continues on the part (V.63526a, Text-fig. 4A).

It is significant that both secondary rachises ($\mathrm{R}_1, \mathrm{R}_2$) converge to the same point on the specimen which corresponds to a broadening of the proximal part of an axis which is continuous with the synangial branch system and could represent the petiole of a small frond (Text-fig. 3B).

Uncovering of the areas around the synangia revealed an extensive branch system which interconnected all eight synangia at the centre of the specimen. The branch is 2·6 mm wide at the base and 43 mm long up to the first T-shaped division (Text-figs 3B, 4A). Distal to this, the axis branches dichotomously three times with internodal distances of 8, 7 and 5 mm respectively. All the divisions are at wide angles except for the most distal which are more acute and bear terminal synangia. Parts of three synangia (nos 34, 35, 36) occur on the right side of the specimen. Their location and orientation suggests an equivalent position on the branch system as the synangia on the left of the specimen.

Organization of the fertile axis

Evidence from the two specimens suggests that the fertile axis is a cruciate branch system characterized by equal, wide dichotomies. This is not at first clear from observing the synangia in V.63525 where only two out of all the penultimate internodes show evidence of axes that have resulted from equal dichotomies and these are distorted and compressed against the synangia themselves. Initial observation of this material suggested a pinnate organization of synangia as suggested by the organization in V.63525 of the branches bearing synangia nos 1–4 and 9–16 (Rowe 1986). Specimen V.63526 demonstrates unequivocal evidence of the cruciate nature of the penultimate internodes.

The apparent 'pinnate' branching of what is essentially a cruciate branch system can be explained taphonomically in terms of the orientation of the branch system relative to the direction of compression during and after deposition and those parts of the branch system distorted as a result. The well preserved segment of V.63526a (Text-fig. 4B) demonstrates the position of eight synangia and the lengths of each internode and their proximal and distal connections very clearly.

One interpretation of this organization suggests that the fertile branch system (comprising groups of 8 synangia) formed canopies, each forming a rectangular surface which was suspended or held erect by the cruciate branch system. It is conceivable that such a structure would have settled distal-surface-down in the sediment. Subsequent distortion of the branch system occurred around the first or second T-shaped divisions which presumably pivoted around to lie in the same plane as the distally placed synangia.

Morphology and orientation of synangia

The synangia are preserved as three-dimensional impressions and show a variety of configurations depending on the orientation of the organ in the matrix prior to compression and the degree of sediment accretion forming around and inside the original structure. Generally the synangia are orientated either laterally or dorsoventrally with respect to the bedding plane (Text-fig. 5).

Laterally orientated synangia have a cone-shaped outline and bear numerous sporangia which emerge from the distal surface (Pl. 3, fig. 5; Text-fig. 5C). Impressions of part and counterpart have similar outlines and each consists of a lateral impression of the synangium wall and a distal fringe of slightly curved sporangia. Blunt-ended projections interpreted as capitate glands emerge from all around the synangium surface apart from the distal surface and are readily distinguished from the acuminate, distal sporangia (Text-fig. 4 D–E).

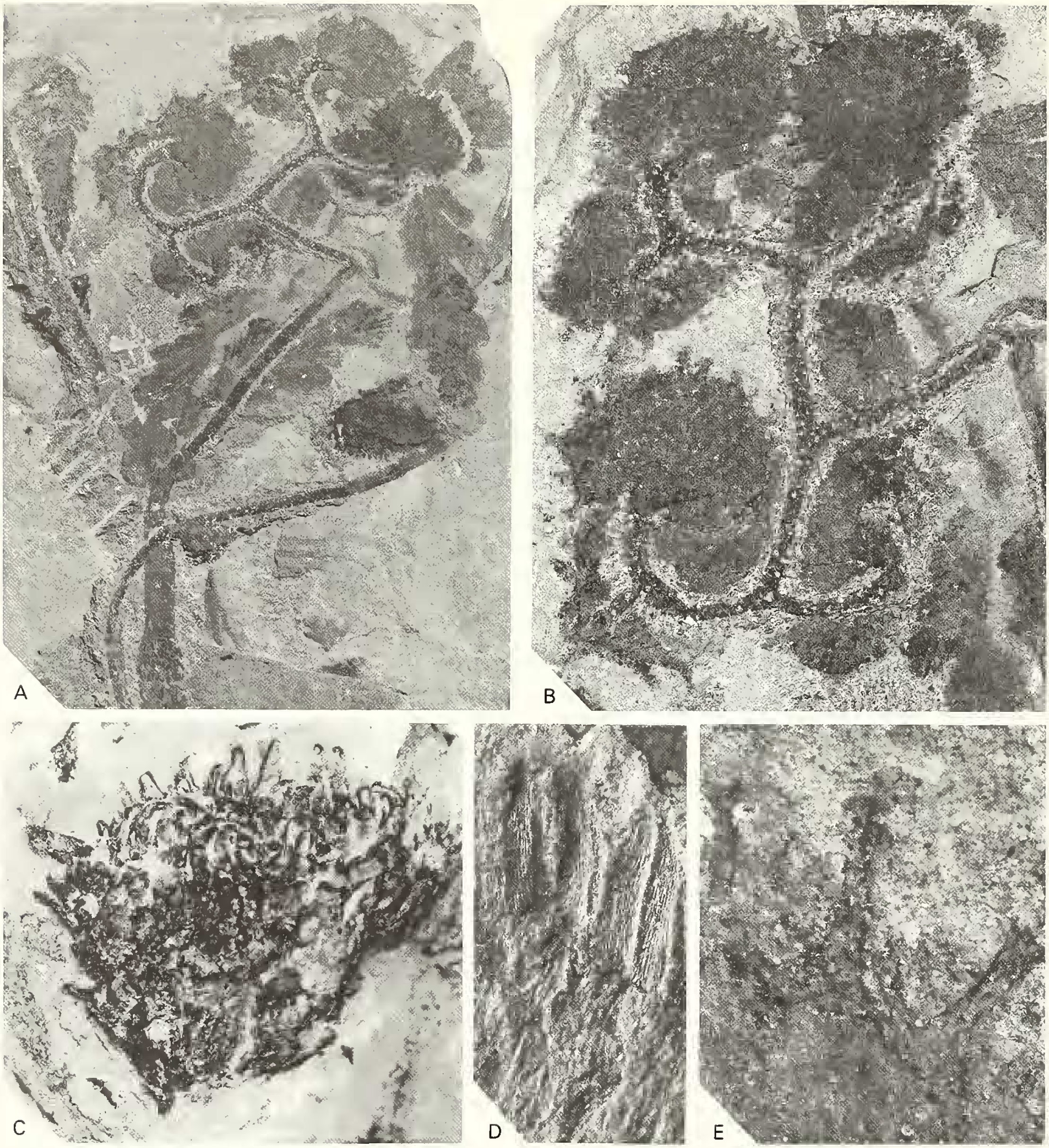
Dorsoventrally orientated synangia show different impression surfaces on part and counterpart of the same synangium. Impressions of the distal surface comprise numerous (8–75) pits which project into the sediment and mark the positions of individual sporangia (Pl. 3, fig. 4; Text-fig. 5B). In nearly all cases the pits are slit-like in surface view and indicate the spaces originally occupied by dehisced or simply flattened sporangia. Where the synangium were not orientated exactly perpendicular to the bedding plane, the pits are oblique and the linear shapes of the sporangia can be distinguished. The proximal surface impressions of dorso-ventrally orientated synangia show completely different surface features. The overall outline of the synangium is oval to circular and the surface is highly rugose (Pl. 3, fig. 3; Text-fig 5A).

Around the margin are broad-based projections which taper in the middle and broaden again at the apex (Text-fig. 4E). These structures are readily distinguished from the apical sporangia (Text-fig. 4D) and are interpreted as stalked capitate glands. They show the same organization in laterally orientated synangia and it is clear that the glands emerge from all around the sides and around the connection to the synangial stalk (Pl. 3, figs 3, 5; Text-fig. 4B, D). Their morphology is corroborated from the study of fusainized specimens described below.

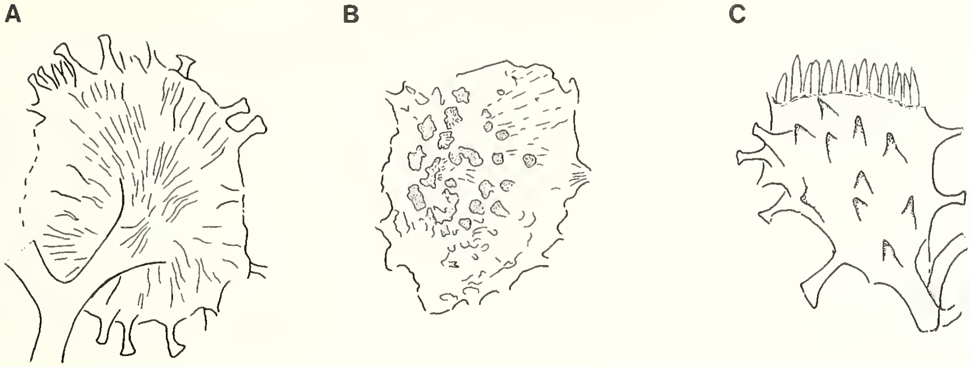
Fine morphology of synangia

The synangia are approximately 7·5 × 6·3 mm. These values represent the means of 31 synangia measured from specimens V.63525a–b and V.63526a–b where the most reliable measurements of length and width came from laterally and dorsiventrally orientated synangia respectively. Synangia were observed to contain 10 to 75 distal sporangia which have a scattered distribution with a tendency to form concentric rows. The sporangia are broad-based and taper to a broad point. The average dimensions are 1·37 × 0·45 mm.

Numerous broad-based glands cover the surface of the synangia. The structures average 0·72–1·72 mm long,



TEXT-FIG. 4. A–E, *Cornutheca glandulosa* gen. et sp. nov. A, V.63526a, extensive fertile branch system undergoing at least 4 dichotomies and bearing 8 terminal synangia (26*a*–33*a*) which are visible as proximal surface impressions. Three additional synangia are present to the right of the first dichotomy of which only one (34*a*) is present on the part. The fructification is intimately associated with two secondary rachises of *Archaeopteridium*, × 1·7. B, enlargement of 8 synangia in A demonstrating four wide-angled, equal dichotomies of the fertile axis, × 3·2. C, V.63527, fusainized synangium orientated laterally to bedding plane, photographed prior to sectioning. Gland bases are visible along the left margin of the synangium and project distally above the numerous, smaller, slightly curved sporangia on the inside, × 5·5. D, V.63525b, distal part of lateral surface impression of synangium (21*b*). Gland base impressions are visible as oblique fissures entering the matrix proximally. The distal margin contains lateral surface impressions of 5–6 sporangia, × 18. E, V.63525a, peripheral margin of proximal surface impression of synangium (7*a*) with three capitate glands, × 20.



TEXT-FIG. 5. Line drawings of three-dimensional impression surfaces of the three main preservational orientations of synangia of *Cornutheca glandulosa*. A, proximal surface impression, V.63525a, holotype (synangium no. 8*a*). B, distal surface impression, V.63526b (synangium no. 30*b*). C, lateral surface impression, V.63525a, holotype (synangium no. 1a), all approx. ×4·0.

0·54 mm wide at the base and taper in the middle (Text-fig. 4E). Distally they average 0·37 mm wide with some specimens having expanded apices up to 0·5 mm wide. The glands cover the outer surface of the synangium and differ from the sporangia which lack distally expanded tips and are confined to the distal part of the synangia. The outer surface of both synangium and glands has a corrugated appearance and consists of axially aligned elements approximately 620–900 μm wide. These elements are far wider than the axially aligned elements on the surface of the sporangia which are approximately 150 μm wide (Text-fig. 4D). About 15–20 glands may be seen on each well-preserved lateral surface and an estimate of the total number for each synangium is 35–40.

Fusainized synangia

Two isolated synangia are preserved as black, three-dimensional material resembling fusain. Both specimens provided sufficient details to prove identity with those described as impressions and also provided additional three-dimensional details of the synangia (Text-fig. 4C; Pl. 4, figs 1–4).

One specimen (V.63527) viewed prior to sectioning (Text-fig. 4C) shows a similar morphology to laterally orientated synangia with evidence of: cone-shaped outline, surrounding wall bearing broad-based glands, distally positioned multiseriate sporangia and rugose surface of synangium wall with evidence of large epidermal cells.

Sections of V.63527 demonstrate a wall layer which surrounds the entire structure (Pl. 4, fig. 4; Text-fig. 6A–G). The wall is 80–120 μm thick and expands outwards locally forming the decurrent bases of the external glands. The development of these gland bases is one of the most striking features of the organ seen in transverse section. In Plate 4, figure 4, six gland bases are visible at varying stages of development. Gland bases are produced at all levels of the synangium and all around the outer surface. The most distal transverse sections (Text-fig. 5G) indicate that the capitate glands may project beyond the distal region of sporangia.

Transverse sections clearly demonstrate an increase in the diameter of the synangium from 7·8 mm at the base up to 10·5 mm at the broadest point just below the level where sporangia are visible externally prior to sectioning (Text-fig. 4C). This corresponds to the outline observed in laterally orientated compressions. At the initiation of each gland base the wall expands outwards and becomes asymmetrically oval in shape. The gland base is decurrent. The centre of each gland encloses a space 125×90 μm to 500×156 μm in diameter which persists for the entire length of the structure. Distally, the glands are polygonal to quadrangular in transverse section.

Similar sections of V.63527 indicate that sediment penetrated the synangium interior and filled all the spaces between and inside individual sporangia. Although individual sporangia were clearly visible in surface view (Pl. 4, fig. 3) their organization is difficult to interpret when seen in transverse section. The sporangia have narrower walls and most have been partly crushed so that adjacent sporangia are flattened against each other. In spite of this, there is some degree of differentiation of wall thickness which may indicate thicker 160 μm (dorsal) and thinner 60 μm (ventral) walls of longitudinally dehiscent sporangia (Pl. 4, fig. 3). The overall size of the internal, distal sporangia and the thickness of their walls readily distinguish them from the relatively massive gland-like structures on the outside and provide a strong argument for distinguishing them morphologically.

The second specimen (V.63528) also shows close morphological similarity with compression specimens. SEM micrographs indicate most significantly that the broadest part of the synangium corresponds to the zone of distal multiseriate sporangia (Pl. 4, figs 1–2). The external surface shows evidence of at least 5 broad gland bases attached to the outer lateral surface of the synangium (Pl 4, fig. 1). These are approximately 0·8–1·1 μm wide and orientated at irregular angles on the synangium surface. Although not well preserved, the synangium wall is entire and encloses 25–30 sporangia. There is some evidence of the large epidermal cells such as those identified on some of the better preserved impressions in V.63525 and V.63526.

Cellular details are not consistently present in either of the fusainized specimens studied. Relatively well-preserved, three-dimensional cells occur towards the outside of the structure in the region of the gland bases (Pl. 4, fig. 4) and crushed or flattened structures with poor cellular details on the inside. Some of the sporangia viewed by SEM as fractured transverse surfaces indicated that the presumed dorsal wall is 5–6 elements (140 μm) thick.

Interpretation of synangium morphology

The interpretation of the structure as a synangiate organ and not an ovulate cupule or some other structure rests on the assumption that the elongate structures on the interior represent sporangia and not sterile lobes or the integument lobes of small ovules. The strongest evidence suggesting the sporangiate nature of the structures is their arrangement which does not resemble the closely radial (even if crushed) arrangement expected if they were integument lobes of ovules, and the asymmetry in thicknesses of what are interpreted to represent dorsal and ventral sporangium walls. Ovules found as isolated units at Drybrook (Rowe 1986) and those found as compressions in other sediments are most often well-preserved proximally in comparison to the relatively delicate integument lobes. None of the compression material or the fusainized specimens shows evidence of dense oval areas indicating the nucellar regions of ovules.

A further problem in the interpretation of this material is the absence of *in situ* spores which, as in all other sporangiate organs from the locality so far, have not survived oxidation from sub-aerial weathering of the sediment.

Genus CORNUTHECA gen. nov.

Type species. Cornutheca glandulosa sp. nov. from the Upper Visean, Drybrook, Great Britain.

Derivation of name. '*Cornus*' (Latin) a horn referring to the horn or cone-shaped outline of the synangium; '*theca*' (Latin) container.

Diagnosis. Synangiate fructification, preserved as compression and fusain, cone-shaped,

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EXPLANATION OF PLATE 4

Figs 1–4. *Cornutheca glandulosa* gen. et sp. nov., Forest of Dean, Upper Visean. 1, V.63528, fusainized specimen showing three dimensional morphology. Lateral surface viewed by SEM. The lower part of the synangium contains at least 3–4 broad oval areas representing fractured gland bases. Numerous sporangia extend from the synangium distally, × 12. 2, distal surface view of synangium in Fig. 1. The continuous wall layer is visible which surrounds approximately 25–30 sporangia, × 12. 3, high power, reflected light micrograph of median section of specimen in Text-figure 4c. Sediment has infilled the structure in and around the sporangia. Note the difference in wall thickness between the gland base in the outer region (arrow 1) and that interpreted as a ventral sporangium wall on the inside (arrow 2), V.63527$7t, × 65. 4, V.63527$8t, composite of reflected light micrographs of transverse section of fusainized synangium approximately half way up from the base. Six glands bases are visible on the left at various stages of differentiation from the synangium wall. The interior contains a complex of thin-walled elements of which some are entire and are interpreted as representing transverse sections through distorted or flattened sporangia, × 32.

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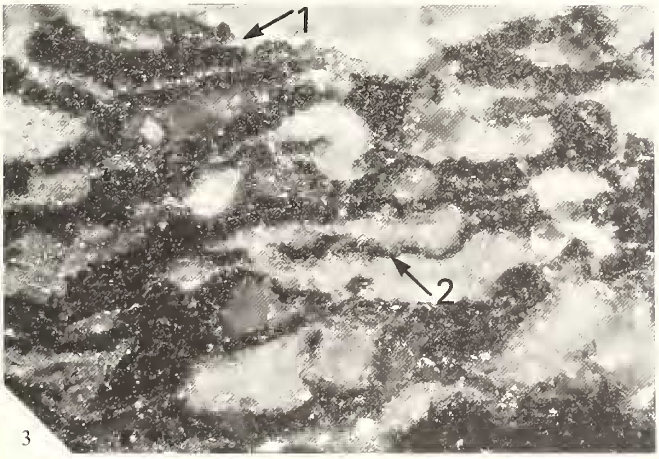

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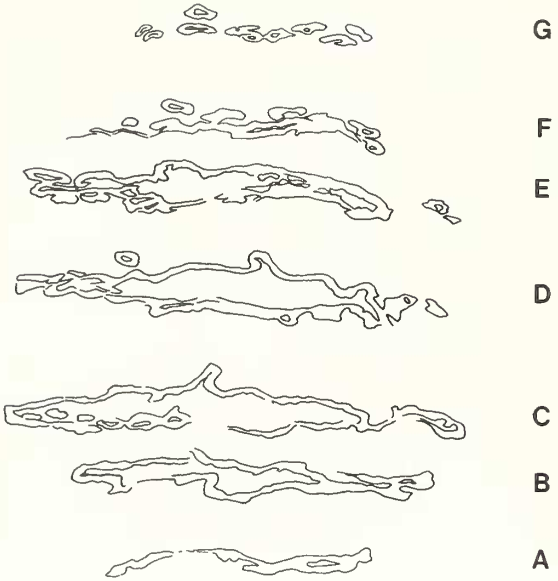
ROWE, *Cornutheca*



TEXT-FIG. 6. *Cornutheca glandulosa*, V.63527. Transverse sections at approximately 0·75 mm intervals of a single fusainized synangium (the letters t, b, refer to the 'top' and 'bottom' of mounted sections/wafers). A, V.63527$12*b*. B, V.63527$11*t*. C, V.63527$8*b*. D, V.63527$8*t*. E, V.63527$7*t*. F, V.63527$6*b*. G, v.63527$4*b*. All ×6.

7·6 × 6·3 mm, consisting of continuous outer wall enclosing 8–75 distal, axially orientated sporangia, 1·3 × 0·45 mm. Outer surface covered with 35 to 40 broad-based, capitate glands approximately 1·72 mm long, 0·5 mm wide at base and up to 0·5 mm wide at apex. Synangia borne terminally on slender, cruciate branch system which undergoes equal dichotomies with subsequent branches separated by 160°–180°. Synangia grouped terminally in symmetrical clusters of 2, 4, 8 and 16 or more. Surface of synangium wall and glands consisting of epidermis with elements, 620–900 μm wide; surface of sporangia marked by axially aligned elements approximately 150 μm wide. Dorsal walls of sporangia 5–6 cells thick.

Cornutheca glandulosa sp. nov.

Plates 3–4; Text-figs 3–6

Derivation of name. '*Glandulosa*' (Latin) referring to the numerous capitate glands covering the outer surface of the structure.

Holotype. V.63525a–b, Pl. 3, figs 1–2, 5; Text-fig. 3A; Text-fig. 4D–E; Text-fig. 5A, C.

Locality. Hazel Hill Quarry, Puddlebrook, near Drybrook, Forest of Dean, Gloucestershire, Great Britain.

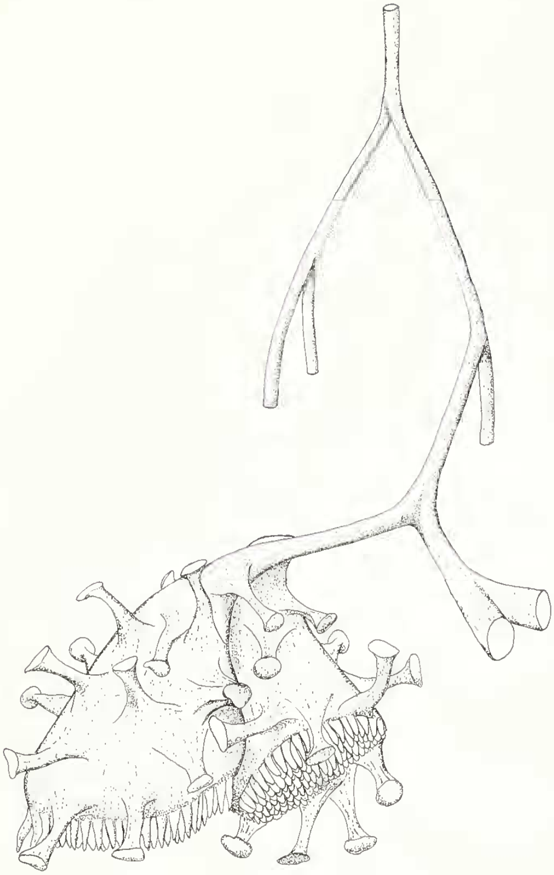
Horizon. Shale band in the Drybrook Sandstone Formation, Lower Carboniferous, Upper Visean (Asbian, NM biozone).

Diagnosis. As for genus. This is the only recognized species.

Reconstruction, comparisons and justification for a new genus

Part of the synangiate branch system is reconstructed in Text-figure 7 based on the four successive distal internodes observed in specimens V.63525a–b and V.63526a–b. The diagram emphasizes the branching of the fertile axis in alternately differing planes and the three-dimensional, multiseriate nature of the synangia. The irregular arrangement of the glands is believed to be correct but the exact morphology of the gland tips is somewhat equivocal.

Previous workers distinguishing genera of synangia have adopted: overall size and shape of synangium, extent of development of the synangium base to which the sporangia are connected, TEXT-FIG. 7. *Cornutheca glandulosa*: reconstruction of pair of synangia attached to segment of cruciate branch system, ×5.



number and arrangement of sporangia, degree of lateral fusion of sporangia, symmetry of synangium in relation to the synangial stalk and pollen content (Benson 1904; Eggert and Taylor 1971; Millay and Taylor 1977; Stubblefield *et al.* 1982; Stidd *et al.* 1985; Galtier 1986; Meyer-Berthaud 1986; Meyer-Berthaud and Galtier 1986; Rowe 1988*c*).

The majority of synangia from Lower Carboniferous sediments consist of a single ring of sporangia fused to some extent laterally and connected basally to an expanded proximal stalk or a pad of tissue. In this level of organization the dorsal surfaces of the sporangia themselves comprise the outer 'wall' or enclosing structure. This organization is seen in *Telangium*, *Telangiopsis*, *Dichotangium*, *Geminitheca*, *Phacelotheca*, *Schuetzia* and *Zimmermannitheca* and has been suggested as characterizing early gymnosperm 'lyginopterid' pollen organs (Millay and Taylor 1979; Stewart 1983). Important exceptions include the synangium described here and a pollen organ from the Upper Visean of Scotland; *Melissiotheca* (Meyer-Berthaud 1986, (see also Bateman and Rothwell 1990)) which has some characters in common with *Cornutheca* (Table 2), including large numbers of multiseriate sporangia inserted in an extensive basal pad of tissue. *Cornutheca* differs from *Melissiotheca* in having an outer wall which surrounds the sporangia distally, in lacking any subdivision of the synangial pad into lobes or sub-lobes and in having a more elongate overall shape. Longitudinal sections of *Melissiotheca* (Meyer-Berthaud 1986, figs 2 (holotype), 16) indicate that the base of the synangium is flatter in profile and that distally the sporangia themselves form the outer limit of the structure. There is also evidence in *Melissiotheca* that the sporangia are grouped in pairs and even groups of four which is apparently not the case in *Cornutheca*. Other characters separating *Cornutheca* include the nature of the synangial stalk which in *Melissiotheca* is massive in comparison to the rest of the synangium and the presence of numerous large capitate glands in *Cornutheca*. These characters distinguish the new material from *Melissiotheca* and all other known Lower Carboniferous synangia. It is therefore believed necessary to distinguish this material at the generic level.

Other synangiate organs from the Drybrook flora include *Dichotangium quadrothecum* (Rowe 1988*c*) and small, simple synangia resembling *Telangium* (Rowe 1986). Interestingly, all three synangia from the same locality represent a range of complexities from the simple ring of sporangia arranged symmetrically around the synangial stalk in *Telangium*, to the more complex expanded synangial pads with a peripheral ring of sporangia in *Dichotangium* and now the most complex which consists of multiseriate sporangia inserted in a basal pad and enclosed in a wall bearing capitate glands. If all these synangia do represent pollen organs of Late Visean gymnosperms they indicate a wide diversity of morphologies which is suggestive of a range of pollen dispersal mechanisms and pollination strategies.

Cornutheca differs from *Dichotangium* at the same locality for the reasons outlined above. Both types of synangia are preserved similarly, as flattened compressions, three-dimensional impressions and fusainized material (Rowe 1988*c*). Further similarities are seen in the range of preservational orientations of both *Cornutheca* and *Dichotangium* with distinct distal, proximal and lateral surface impressions. In *D. quadrothecum* some of the preservational variants (Rowe 1988*c*, figs 41–42, 44–45) show superficial similarities with the proximal impression surfaces of *Cornutheca* (Pl. 3, figs 3–5). However, in addition to the overall differences in size of the synangia and sporangia (Table 2) the smaller more condensed groups of *Dichotangium* synangia lack multiseriate sporangia on proximal impression surfaces and lack any indication of a surrounding wall which in *Cornutheca*, encloses at least the lower halves of the sporangia.

Relationship of Cornutheca *to* Archaeopteridium

Cornutheca is known from only five specimens of which two are large, extensively branched and superimpose fronds of *Archaeopteridium*, also very rare at the locality. The total finds of *Archaeopteridium* and *Cornutheca* probably represent only 1–2% of all identifiable plant specimens extracted from the locality. In spite of the large numbers of stems, foliage and reproductive organs at Drybrook, attempts at reconstructing whole plants are hampered by the high degree of fragmentation. In view of the extremely low numbers of frond and synangium specimens, the fact that both synangiate branch systems in V.63525 and V.63526 superimpose what are probably bifurcate fronds provides the most compelling evidence that both taxa represent parts of the same plant. If such is the case, judging from the overall size of the fertile branch system, it seems likely that the fertile portion did not replace a group of pinnules or a pinna segment of one of the secondary rachises of the *Archaeopteridium* frond, but was perhaps connected to the stouter petiole, possibly as a median cauline branch of a trifurcate division. This is suggested to some extent by the orientation of the fertile branch to the secondary rachises and possibly proximal petiole in V.63526 (Text-fig. 3B).

The majority of Lower Carboniferous synangia are known only from isolated synangia. Evidence of the synangial/sporangial branch system and its relation to vegetative fronds among putative early gymnosperms has been observed principally in compression material (Walton 1926, 1931; Eggert and Taylor 1971; Jennings 1976; Skog and Gensel 1980).

Meyer-Berthaud (1989) divided the known sporangiate/synangiate branch systems and associated/connected fronds into four groups. These included (A) presumed ancestral progymnosperms with sporangia borne on branched fertile axes, (B) putative gymnosperms; *Triphyllopteris* and *Rhacopteris fertilis* where sporangial clusters are attached and occupy the terminal portion of an otherwise vegetative frond, (C) plants with *Telangium*/*Telangiopsis*-type synangia where stalked synangia replace vegetative clusters of pinnules on otherwise extensive vegetative, pinnate fronds, and (D) plants with a *Diplopteridium*-type of organization where synangia are borne terminally on a dichotomous branch system which lacks foliage and is borne medianly on a trifurcate frond.

TABLE 2. Summary of main characters of four 'complex' synangiate organs from the Upper Visean of the British Isles (measurements in mm).

	Cornutheca glandulosa	*Dichotangium quadrothecum*	*Melissiotheca longiana*	*Phacelotheca pilosa*
Length × width	7·6 × 6·3	1–2·5 diam.	3·0 × 4·3–6 × 4·5	1·5–2·0 long
Organization	Cone-shaped, wall with capitate glands enclosing numerous sporangia	Oval synangial pads bearing marginal fringe of sporangia	Lobbed parenchymatous cushion bearing many sporangia on distal surface	Up to eight aggregated synangia borne on 'telescoped' branch system
No. sporangia	9–75	12–24	50–150	Approx. 30 to each cluster, 2–4 to each synangium
Size of sporangia	1·3 × 0·45	1·8–2·2 × 0·3–0·55	2·0 × 0·28–0·35	1·3–1·5 × 0·35–0·55
Structure of sporangia	Broadly pointed dorsal wall, 5–6 layers of cells with sclerenchyma, ventral wall thinner	Beaked, dorsal wall, 2–4 layers with sclerenchyma ventral wall thin	Recurved, pointed, cylindrical, dorsal wall thick, ventral wall thin	Pointed, with surface hairs, dorsal wall thick ventral wall thin
Stalk tracheids	—	Scalariform	Scalariform	Scalariform
Branch system	Cruciate, isotomous	Cruciate, isotomous	Unknown	Possibly attached to pinnate *Lyginorachis*
Locality/age	Drybrook Sst., Drybrook, W. England: U. Visean	Drybrook Sst, Drybrook, W. England: U. Visean	U. Oil Shale Group, Kingswood, nr. Pettycur, Scotland: U. Visean	U. Oil Shale Group, Kingswood, nr. Pettycur, Scotland: U. Visean

The new material from Drybrook comprises extensive branch systems which lack vegetative foliage and consist entirely of dichotomizing axes with terminal synangia. There is no direct evidence of how this branch system was borne on the parent plant but it is assumed that it would fall into the category of (B) or (D) of Meyer-Berthaud (1989). Until more is known about the *Archaeopteridium*/*Cornutheca* relationships and exactly how fertile branch systems are connected to frond petioles, an equivocal hypothesis would suggest a trifurcate arrangement as seen in a number of Upper Visean gymnosperm leaves (Walton 1931; Long 1976, 1979*a*, 1979*b*; Galtier and Scott 1986; Rowe 1988*c*).

Evolutionary trends and complexity among Lower Carboniferous synangia

Among Lower Carboniferous putative gymnosperms there is now growing evidence of complex synangiate organs with large numbers of sporangia. *Cornutheca* and *Melissiotheca* had evolved extensive synangial pads to accommodate multiseriate sporangia. *Phacelotheca* (Meyer-Berthaud and Galtier 1986) evolved a highly divided distal branch system where, although each terminal branchlet bears relatively few sporangia, the branches are orientated in the same direction and form a compact mass. *Dichotangium* is somewhat intermediate with enlarged distal pads and sporangia that are confined to the peripheral margin.

Complex synangia show advantages over the simple sporangiate branches of aneurophytalean progymnosperms and the most simple putative gymnosperm synangia represented by the *Telangium* type. These include the obvious advantage of increasing the total number of sporangia and spore/pollen output for a given axis/frond/leaf, while in forms such as *Cornutheca*, *Dichotangium* and *Telangiopsis bifida* a dichotomous branch system producing synangia at the same level of ontogeny (i.e. distally) would have the advantage of producing simultaneously the pollen output from numerous synangia to coincide with favourable periods of likely pollination.

A further consideration concerns the morphological relationship of the type of fertile branch system observed in synangiate organs listed in the second possibility above with putative ancestral aneurophytalean fertile axes. The discovery of *Cornutheca* and its extensive branch system provides another example, like *Dichotangium*, of a more complex fructification borne on a simple cruciate branch system. At first this seems to raise a paradoxical situation where a highly evolved, complex synangium is borne on a primitive axis. One explanation of this combination of characters is that an ancestral, cruciate system of axes presumably derived from progymnospermous/earliest gymnosperm ancestors required little morphological change to fulfil selected requirements of increasing pollen output while satisfying other ecological requirements for successful pollination biology. The latter may involve the advantages listed above and may result from either better wind dispersal from a localized branch system independent of nearby foliage, or from the possibility of possessing a dense target area (Skog and Gensel 1980) attracting foraging arthropods which may have played a role in aiding dehiscence, liberation and/or transfer of pollen.

Of additional interest are the structures interpreted as capitate glands which surround the outside of the synangium wall. Hairs, spines and glands are known sporadically on Palaeozoic gymnosperm reproductive organs. Lower Carboniferous seeds and pollen organs are so far known only to possess hair or spine-like emergences (e.g. Meyer-Berthaud and Galtier 1986; Galtier and Rowe 1989). Definite glandular structures are more common in the Upper Carboniferous where the best documented cases include stalked capitate glands on stems and rachises of *Lyginopteris* and single ovulate cupules of *Lagenostoma lomaxii* (Oliver and Scott 1904) and the glandular structures on callistophytalean stems and pollen organs (Rothwell 1975).

Acknowledgements. This work was carried out in several laboratories over a number of years and is part of a long-term investigation into early gymnosperms. Funding for this research is acknowledged from the NERC (UK) and the Alexander von Humboldt organization (Germany). The author is grateful to Dr C. J. Cleal for constructive criticism of the manuscript.

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Typescript received 29 July 1991
Revised typescript received 19 December 1991